

Living on the edge: Habitat and host-plant selection in the butterfly *Lycaena tityrus* (Lepidoptera: Lycaenidae) close to its northern range limit

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Abstract. We here investigate habitat preferences and its variation between the sexes as well as oviposition site selection in a population of the Copper butterfly *Lycaena tityrus* in North-East Germany. Within a continuous habitat, butterflies preferred locations characterized by a higher abundance of nectar plants and a higher proportion of bare ground than found at random, stressing the pivotal importance of adult income and favourable microclimatic conditions. No differences in habitat selection could be detected between males and females, indicating a lack of mutual interference e.g. through male harassment, which is attributed to the relatively low abundance of butterflies in the study area. Females preferentially selected the lowest parts of relatively small (= young) host-plants, growing within relatively low vegetation or in the vicinity of bare ground, for oviposition. Thus, females seem to select high-quality plants and deposit their eggs in the warmest microhabitats available. We suggest that selecting warm microhabitats is an important adaptation for the species' survival under limiting climatic conditions, which is the case for the population studied here being found close to the species' northern distribution limit.

Key words: adult income, habitat preference, habitat quality, host plant, Lycaenidae, microclimate, oviposition.

INTRODUCTION

The general needs of any given species can be characterized as a specific set of resources including consumables (such as host-plants) and utilities (such as perch structures; Dennis *et al.*, 2006; Bauerfeind *et al.*, 2009). The presence and abundance of the above resources determines whether a certain habitat patch may or may not support a population of a focal species (Maes *et al.*, 2006; Dennis & Hardy, 2007). However, apart from providing the basic requirements which in

either case need to be met, habitat patches may show strong variation in habitat quality. Such differences may crucially affect larval and adult survival, thereby affecting population dynamics (Weiss *et al.*, 1993; Friberg *et al.*, 2008; Turlure & Van Dyck, 2009; Van Dyck & Regniers, 2010). The ability to discriminate between more or less favourable habitats is therefore of pivotal importance for the long-term survival of populations ('preference-performance hypothesis'; e.g. Bonebrake *et al.*, 2010). Unfortunately though, for many if not most species we are currently not able to completely resolve the specific factors involved in determining habitat quality as a crucial prerequisite for successful habitat management (Dennis *et al.*, 2006; Maes *et al.*, 2006; New, 2007 and references therein).

When trying to determine habitat quality, complications may arise from differences in habitat requirements and preferences among sexes (Parker, 1978; Wiklund, 2003; Croft *et al.*, 2006). For instance, the distribution of female butterflies depends on the occurrence of host plants for oviposition (Turlure & Van Dyck, 2009), a factor that is largely irrelevant to males. Also the relevance of other resources such as nectar for adult feeding may differ between the sexes (Fischer & Fiedler, 2001a, 2001b; Turlure & Van Dyck, 2009). Male distribution, on the other hand, should be most strongly affected by the occurrence of receptive

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females. However, male mate location behaviour may in turn impact on female distribution (Parker, 1978). At least in some species females disperse away from areas of high male density in order to avoid male harassment, which may largely exclude females from otherwise suitable habitat (Baguette *et al.*, 1998, Wiklund *et al.*, 2001; Turlure & Van Dyck, 2009).

Finally, it has long been known that larval and adult habitat requirements may strikingly differ (Wiklund, 1977; Dennis *et al.*, 2006). Often, larval habitat requirements are more limiting to population persistence than adult requirements (Elmes & Thomas, 1992; Thomas *et al.*, 2001; Anthes *et al.*, 2003; Wynhoff *et al.*, 2008; Dierks & Fischer, 2009), which has been often overlooked in the past, at least partly because the ecology of pre-imaginal stages is more difficult to observe. Nevertheless such potential differences add further complication to the assessment of a species' habitat requirements.

Against the above background we here investigate (micro-)habitat preferences in the Copper butterfly *Lycaena tityrus* by (1) comparing occupied and vacant habitat patches within a continuous habitat, by (2) investigating potential differences in habitat selection between males and females, and by (3) analyzing oviposition site selection. *L. tityrus* occurs throughout large parts of Eurasia (Tolman & Lewington, 1998). In central Europe it is nowadays a fairly rare species with documented population declines in several regions (Ebert & Rennwald, 1991). Population declines are mainly driven by *L. tityrus* inhabiting different types of grassland, which were subject to substantial agricultural intensification over recent decades.

MATERIALS AND METHODS

Study organism

Lycaena tityrus is a widespread temperate-zone butterfly, ranging from Western Europe to central Asia (Ebert & Rennwald, 1991; Karl *et al.*, 2008). The species is bivoltine with two discrete generations per year in most parts of its range, although populations with one or three generations per year occur (Ebert & Rennwald, 1991; Tolman & Lewington, 1998). *L. tityrus* colonizes different types of unimproved anthropogenic grassland as well as natural grassland such as swampy clearings or mountainous canyons and ridges (Karl & Fischer, 2009). The principal larval host-plant is *Rumex acetosa*, but some congeneric plant species such as *R. acetosella* and *R. scutatus* are utilised as well (Ebert & Rennwald, 1991; Tolman & Lewington, 1998; Karl *et al.*, 2008). The eggs are laid singly on the base of the leaf stem or on the leaf

itself (SBN, 1994). Adult butterflies predominantly feed on flowers of composite plants (Asteraceae), but seem to be fairly opportunistic with regard to nectar plant use (Ebert & Rennwald, 1991; Karl & Fischer, 2009). The study was conducted on a relatively dry and sandy fallow field (ca. 40 ha), being currently mown once a year without removing the hay, near the town of Greifswald in North-East Germany. The field work was carried out between May 13th and June 17th during the first and between July 31st and August 15th during the second flight period 2009.

Habitat selection of adult butterflies.

For analysing habitat preferences the following parameters were recorded: slope (in degrees from 0-90°), exposition (in degrees from 1-360°, with 0/360° indicating exposure to the north, 90° exposure to the east etc.), wind exposure (in 3 classes: 1 = sheltered from wind, 2 = intermediate, 3 = strongly wind-exposed), percentage of bare ground in vertical projection, number of vascular plant species, percentage of ground covered by *Rumex* (oviposition) plants, number of *Rumex* plant individuals, availability of nectar flowers (in classes from 0-9, with 0 indicating a lack of flowers and 9 an abundance of flowers), and average vegetation height (as a mean of 16 random, individual measurements). During the first generation, the above parameters as well as *L. tityrus* numbers were scored on 42 randomly selected plots of 5 x 5 m², half of which were occupied by butterflies, while the other half was unoccupied during field work. Plot occupation was determined by inspecting each plot repeatedly during the flight period. While in all occupied plots (resting) individuals were repeatedly observed, plots without any *L. tityrus* observation were classified as unoccupied. Records of some of the above parameters, namely percentage of bare ground, number of vascular plant species, percentage of ground covered by *Rumex* plants, and number of *Rumex* plant individuals, were not based on entire plots, but were restricted to four standardised 1 m² sub-plots per 25 m² plot (for time reasons). In these cases mean values were used for further analysis.

While the above data allowed for a comparison between occupied and vacant patches (within the study area), differences in habitat preferences between the sexes were investigated in the second generation. Therefore, we searched the study area for male and female *L. tityrus* butterflies (n = 31 each). When a butterfly was found, we scored the parameters listed above within plots of 1 m², with the place of encounter serving as centre. Habitat parameters were scored as outlined above, except that throughout no sub-plots

were used and that vegetation height was measured at 4 random places within the 1 m² plots only.

Oviposition site selection.

For investigating oviposition site preferences individual *L. tityrus* females were followed until they had deposited an egg. Habitat parameters were subsequently scored using the plant chosen for oviposition and a randomly selected, adjacent control *Rumex* plant. In the first generation the parameters measured included distance of the egg from the ground, *Rumex* plant height, length of the (nearest) *Rumex* leaf the egg was laid on (or length of a randomly selected leaf for control plants), height of the surrounding vegetation (mean within a 20 cm radius), and the percentage of bare ground. In the second generation the number of leaves per *Rumex* plant and ambient temperature 1, 10 and 20 cm above ground (next to the plant, measured with a thermocouple) were recorded additionally. As during the whole study butterflies were not marked, we cannot rule out that we occasionally used the same individuals (also above). However, given the size of the whole study area and the size of the population it is highly unlikely that potential double counts significantly affected the results presented here.

Statistical analyses

Comparisons between vacant and occupied patches, male and female habitats, and between oviposition and random *Rumex* plants were analysed using Mann-Whitney U-tests. To further analyse habitat preferences we used general non-linear models (GNLMs) with a binomial (comparing occupied and vacant patches) or ordinal (comparing vacant patches with ones inhabited by a single or more than one butterfly) error distribution. Differences in temperature at the three heights above ground were tested by a Kruskal-Wallis test. Distributions of butterfly eggs across plant height classes were tested against even distributions by chi-square tests. All statistical tests were performed by using Statistica (8.0) and SPSS for Windows (17.0 Student Version).

RESULTS

Habitat preferences of adult butterflies

Only one of the parameters investigated differed between patches occupied by *L. tityrus* and randomly selected patches (Table 1a). The number of nectar

flowers available to butterflies was significantly higher in occupied than random patches. However, even the latter difference would be non-significant when applying a Bonferroni correction to the results. When we analyzed the data using a GNLM with a binomial error distribution, we found that the percentage of bare ground ($\chi^2_1 = 7.0$, $p = 0.008$) and flower availability ($\chi^2_1 = 3.8$, $p = 0.052$) were the strongest predictors of butterfly occurrence, with the probability of occurrence increasing with a higher percentage of bare ground and higher flower numbers. When using a GNLM with an ordinal error distribution, thus comparing vacant patches with ones inhabited by a single or more than one butterfly, flower availability ($\chi^2_1 = 4.6$, $p = 0.031$) turned out to be the strongest predictor of butterfly numbers followed by the percentage of bare ground ($\chi^2_1 = 3.1$, $p = 0.079$). No sexual differences in habitat preferences were detected in second generation butterflies (Table 1b).

Oviposition site preferences

In the first generation, *R. acetosa* plants used for oviposition were significantly smaller than randomly selected *R. acetosa* plants, and the surrounding vegetation was significantly lower at oviposition compared to random sites, while the other two parameters investigated did not differ significantly (Table 2a). The data from the second generation also indicated a significant preference for smaller *R. acetosa* plants, while differences in the height of the surrounding vegetation were not significant here (Table 2b). However, the percentage of bare ground at oviposition sites was significantly higher than at random sites. The remaining parameters, including temperatures measured at different heights above the ground, did not differ significantly between oviposition and randomly selected *R. acetosa* plants. However, temperature decreased significantly with increasing distance from the ground ($H_2 = 89.1$, $p < 0.0001$; Table 2b).

In addition to preferring smaller *R. acetosa* plants for oviposition (see above), *L. tityrus* females deposited the vast majority of their eggs quite close to the ground, i.e. between 0 and 5 cm above ground (significant deviation from an even distribution across height classes; $\chi^2_2 = 55.6$, $p < 0.0001$; Fig. 1a). This pattern was not per se caused by preferring small plants. Females clearly preferred to oviposit on the lowest parts of host plants, as indicated by measuring the position of eggs relative to plant height (significant deviation from an even distribution across height classes; $\chi^2_3 = 35.2$, $p < 0.0001$; Fig. 1b).

Table 1. Comparison of various habitat parameters (means \pm SE) between random and occupied (by *Lycaena tityrus*) patches (a; n = 21 each), and between encounter sites of male versus female butterflies (b; n = 31 each). Significant p-values, as tested by Mann-Whitney U-tests, are given in bold.

Parameter	Random		Occupied		Z	p
	Mean	SE	Mean	SE		
Slope [°]	1.4	1.1	1.7	1.5	0.23	0.8155
Exposition [°]	203.1	88.0	154.4	80.0	-1.70	0.0893
Wind exposure	2.1	0.8	1.8	0.9	-1.29	0.1955
Bare ground [%]	7.2	6.1	13.4	15.8	0.40	0.6869
Plant species [n]	17.6	3.5	19.1	4.6	0.87	0.3838
<i>Rumex acetosa</i> [%]	8.6	5.3	9.9	10.2	-0.53	0.5971
<i>Rumex acetosa</i> [n]	19.5	8.3	15.7	10.2	-1.41	0.1588
Flowers [n]	1.7	1.2	2.7	1.8	2.45	0.0144
Vegetation height [cm]	15.0	8.5	13.8	9.2	-0.58	0.5621

Parameter	Random		Occupied		Z	p
	Mean	SE	Mean	SE		
Slope [°]	0.9	0.8	0.7	1.0	1.16	0.2055
Exposition [°]	217.7	99.3	196.0	99.6	0.96	0.3359
Wind exposure	1.8	0.8	1.8	0.6	-0.34	0.7111
Bare ground [%]	5.9	11.7	6.8	11.1	-0.95	0.3153
Plant species [n]	11.6	3.3	11.7	2.8	0.07	0.9436
<i>Rumex acetosa</i> [%]	7.0	7.5	7.5	5.6	-0.97	0.3292
<i>Rumex acetosa</i> [n]	16.0	13.1	19.1	12.8	-0.98	0.3274
Flowers [n]	2.5	2.3	2.5	2.2	0.08	0.9314
Vegetation height [cm]	11.5	10.6	11.5	11.6	0.99	0.3191

DISCUSSION

Within the continuous habitat investigated, very few differences between specific sites occupied or not occupied by *L. tityrus* butterflies could be detected. The only significant predictors of butterfly occurrence in our study were flower availability and the percentage of bare ground. The importance of flowers is hardly surprising, as nectar plays a crucial role in butterflies as flight fuel, and for prolonging longevity and increasing reproductive output (Rusterholz & Erhardt, 2000; Fischer *et al.*, 2004; Bauerfeind & Fischer, 2005). The related Copper butterfly *L. hippothoe* L., for instance, has been shown to rely particularly strongly on nectar intake for egg production (Fischer & Fiedler, 2001a). Accordingly, field studies have shown that availability of nectar

plants is positively related to both the number of butterfly species and the number of individuals within species (Feber *et al.*, 1996; Fred *et al.*, 2006; Pyöry *et al.*, 2009).

The preference for places with a higher proportion of bare ground and thus a more heterogeneous vegetation structure is most likely related to beneficial microclimatic conditions. Temperature near the ground is also affected by solar radiation and wind exposure. Associated parameters, however, did not differ significantly between occupied and random patches (Table 1a), probably as a result of the relative homogeneity of the study area with respect to these factors. The same reasoning may apply for the lack of an association between butterfly occurrence and host plant abundance, as *Rumex* plants are abundantly available throughout the whole study area. However,

Table 2. Comparison of various parameters (means \pm SE) between *Rumex acetosa* plants used by *Lycaena tityrus* for oviposition and randomly selected (*R. acetosa*) plants in the first (a; n = 22 each) or second flight period (b; n = 30 each). Significant p-values, as tested by Mann-Whitney U-tests, are given in bold.

Parameter	Oviposition		Random		Z	p
	Mean	SE	Mean	SE		
Plant height [cm]	17.8	3.3	28.9	3.3	-2.84	0.0045
Leaf length [cm]	5.0	0.3	5.1	0.3	-0.21	0.8327
Vegetation height [cm]	20.1	2.2	28.3	2.2	-2.79	0.0052
Bare ground [%]	39.5	4.5	43.2	4.5	0.46	0.6472

Parameter	Oviposition		Random		Z	p
	Mean	SE	Mean	SE		
Plant height [cm]	14.4	2.4	21.4	2.4	-2.95	0.0032
Leaves [n]	5.7	0.5	4.7	0.5	1.23	0.2170
Leaf length [cm]	4.0	0.4	4.9	0.4	-1.53	0.1260
Vegetation height [cm]	18.9	1.7	20.9	1.7	-1.13	0.2581
Bare ground [%]	55.0	3.7	38.5	3.7	-2.92	0.0035
Temperature 1 cm [°C]	30.3	0.5	29.7	0.5	0.82	0.4119
Temperature 10 cm [°C]	26.6	0.3	26.1	0.3	1.13	0.2581
Temperature 20 cm [°C]	25.4	0.3	24.7	0.3	1.77	0.0773

spots of bare ground will warm up more quickly and reach higher equilibrium temperatures compared to ground covered by vegetation, such that these spots are likely to represent the warmest places within our study area. As temperate-zone butterflies typically prefer the warmest spots within their habitats (e.g. Thomas & Lewington, 2010), we believe that the preference for bare ground is caused by its higher temperature.

A bit surprisingly, no differences in habitat selection between male and female *L. tityrus* butterflies could be detected, while studies on other butterflies including lycaenids have shown sex-specific differences (e.g. Baguette *et al.*, 1998; Rusterholz & Erhardt, 2000; Wiklund *et al.*, 2001; Turlure & Van Dyck, 2009). Obviously, both sexes prefer both flower-rich areas and favourable microclimates, without a significant mutual interference between the sexes. The lack of mutual interference is probably caused by the relatively low population density in the study area compared with other *Lycaena* populations (Fischer *et al.*, 1999; Fischer & Fiedler, 2001b). An equally strong preference for nectar plants across sexes is conceivable as both sexes rely on adult income for

flight and increased life span (see above). While females furthermore need nectar for egg production, males may set up their territories close to nectar plants awaiting receptive females. Such resource-based territoriality has been shown for *L. hippothoe* (Fischer & Fiedler, 2001b; Turlure & Van Dyck, 2009), and may also exist in *L. tityrus*. The lack of a difference in host-plant abundance at male and female encounter sites is most likely once again related to the abundant and homogeneous occurrence of *Rumex* in the study area.

Our data on oviposition site selection revealed that females clearly preferred to oviposit on fairly small host-plants, on which they deposited their eggs close to the ground (*cf.* Singer & McBride, 2010; Thomas & Lewington, 2010). Females were repeatedly observed to alight on a host-plant, after which they climbed down to reach the parts of the plant close to the ground. While the preference for smaller (= younger) plants is probably related to their higher nutritional quality for hatching caterpillars (more nutrients, fewer secondary plant products; e.g. Begon *et al.*, 1996), the preference for the plants' lower parts is likely to be related to higher temperatures close to the

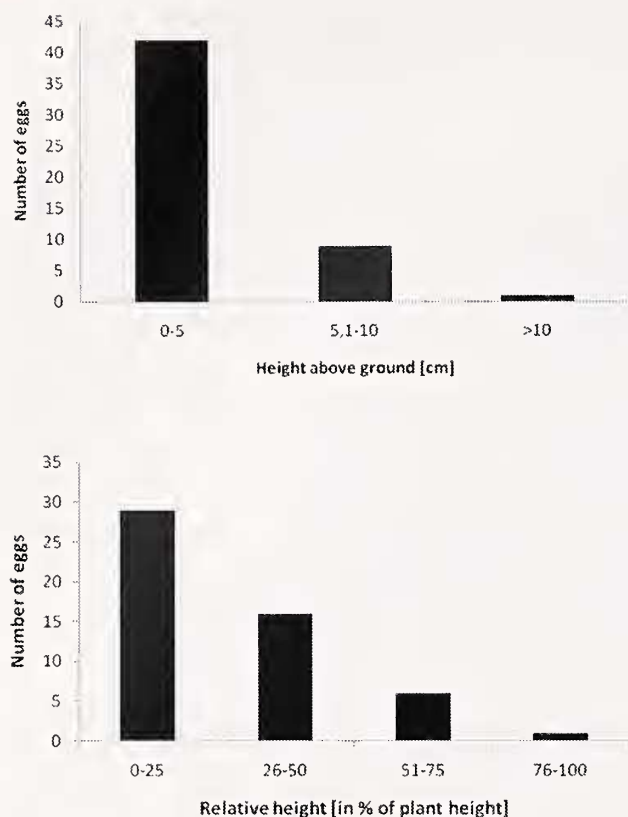


Figure 1. Position of *Lycaena tityrus* eggs on *Rumex* plants as measured as absolute height above ground (a) and relative height in % of total plant height (b; n = 52 each).

ground (cf. Table 2b). Such conditions will evidently speed up development. A comparable behaviour was not observed in *L. tityrus* populations in southern Germany or northern Italy, where eggs are laid higher above the ground (KF, personal observations). We therefore hypothesise the existence of population-specific differences in oviposition behaviour, with the females from the population investigated here, which is close to the northern limit of the distribution range of *L. tityrus*, selecting the warmest places for oviposition under relatively poor climatic conditions (Thomas, 1990). Alternatively, such behavioural differences may arise as a consequence of plasticity in oviposition site selection (Gibbs & Van Dyck, 2009).

The findings that lower vegetation (first generation) and bare ground (second generation) were preferred for oviposition further support the notion that *L. tityrus* females prefer warmer sites for egg-laying. Note in this context that the field was mown between the first and the second flight period, which explains why there was no longer a significant effect of vegetation height in the second generation. Why the percentage

of bare ground had no significant influence on oviposition site selection in the first generation is unclear, but might be related to the approaching cooler (autumn) conditions after the second flight period. In order to ensure that larvae will reach their hibernation stage before winter, females may have been even more selective in the second generation (cf. Thomas & Lewington, 2010 for *Polyommatus bellargus*).

In summary, we found little evidence for pronounced site selectivity in adult *L. tityrus* butterflies within a continuous habitat. Butterflies preferred warm locations rich in nectar plants. However, investigating oviposition plant selection revealed more clear-cut patterns, with females preferring to oviposit on small, high-quality plants and actively seeking to deposit their eggs in warm microclimates. The latter might be a crucial and therefore widespread adaptation in butterflies occurring in cooler climates, as is the case for the *L. tityrus* population studied here which occurs close to the northern limit of the species' range.

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